RESEARCH REPORT

07

Genetics of Interior Spruce in British Columbia: Performance and Variability of Open-pollinated Families in the East Kootenays

C.-Y. Xie

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1998

BRITISH COLUMBIA

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Canadian Cataloguing in Publication Data
Xie, Chang-Yi, 1957-
Genetics of interior spruce in British Columbia: performance and variability of open-pollinated families in the East Kootenays

(Research report ; 07)

Includes bibliographical references: p.
ISBN 0-7726-2839-4

1. Engelmann spruce - British Columbia - Growth. 2. White Spruce - British Columbia - Growth. 3. Engelmann spruce - British Columbia - Seedlings - Evaluation. 4. White Spruce - British Columbia - Seedlings - Evaluation. 5. Engelmann spruce - Ecophysiology - British Columbia. 6. White Spruce - Ecophysiology - British Columbia. I. Yanchuk, Alvin D. (Alvin Dale), 1957- II. Kiss, G.K. III. British Columbia. Ministry of Forests. Research Branch. IV. Title. V. Series: Research report (British Columbia. Ministry of Forests. Research Branch) ; 07.

SD397.S.S77X53 1998 634.9'752562 C96-960084-4

© 1998 Province of British Columbia
Published by
Forestry Division Services Branch
Production Resources
595 Pandora Avenue
Victoria, BC V8W 3E7

Copies of this and other Ministry of Forests titles are available from
Crown Publications Inc.
521 Fort Street
Victoria, BC V8W 1E7

ABSTRACT

The performance and variability of 110 open-pollinated interior spruce families from the East Kootenays in southeastern British Columbia were investigated at 10 local sites and one site at Red Rock, near Prince George. Twenty years after outplanting, spruce reached an average height, diameter, and stem volume of 354 cm, 51 mm, and 5247 cm^3, respectively, and demonstrated an exponentially shaped height growth curve. The average survival was 73%, with more than 85% of the mortality occurring during the first three years after outplanting. Differences among test sites were highly significant ($p<0.0001$) in both growth and survival, and accounted for most of the observed variation. Among family variation in growth and survival was also highly significant. Spruce originated from calcareous soil tended to be superior wherever they were planted, and trees grew significantly faster and survived better at acidic sites regardless of their origin. Genetic differentiation along elevation was strongly clinal, and the performance of the East Kootenay families at Red Rock was excellent. Transferring seed sources more than 230 m up or more than 150 m down in the East Kootenays is not recommended, but East Kootenay materials may be successfully used for reforestation at locations as far as 4 degrees northwards and 7 degrees westwards from their average origin. The results also point to the need for adequate site preparation, and quality stock raising, handling, and planting, as well as controlling weed competition for reforestation success.

ACKNOWLEDGEMENTS

We are grateful to D. Wallden for data collection and field assistance. Comments from Drs. R.D. Burdon and C.C. Ying are also greatly appreciated.

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INTRODUCTION

White and Engelmann spruce (*Picea glauca* (Moench) Voss and *P. engelmannii* Parry, respectively) form a complex of sympatric and allopatric populations covering the interior portion of British Columbia. Because of intensive introgressive hybridization, these two species cannot be easily distinguished morphologically, physiologically, or chemotaxonomically (Roche 1970). Even their wood is almost identical in appearance, durability, and strength properties, and thus is used interchangeably (Barton and Gardner 1957). Owing to the biological and economic similarities of these two species, the white-Engelmann spruce complex is referred to as interior spruce in British Columbia for management convenience.

Interior spruce is the most commonly planted tree "species" in British Columbia and has the greatest value to the forest economy of the province. The British Columbia Ministry of Forests initiated an ambitious interior spruce breeding program in the late 1960s aimed at producing sufficient quantities of genetically improved seeds to meet the regeneration demand. This program started with designating three selection units (East Kootenay, Prince George, and Prince Rupert Selection Units) across the white-Engelmann spruce complex, based mostly on biogeoclimatic information (Figure 1). Environmental conditions within units were believed to be homogeneous; thus, selected materials may be interchangeable. In each unit, desirable phenotypes (plus-trees) were selected and their genetic merit was tested in open-pollinated progeny trials. The present report is a summary of 20-year test results on the performance and variability of the selected open-pollinated families in the East Kootenay Selection Unit.

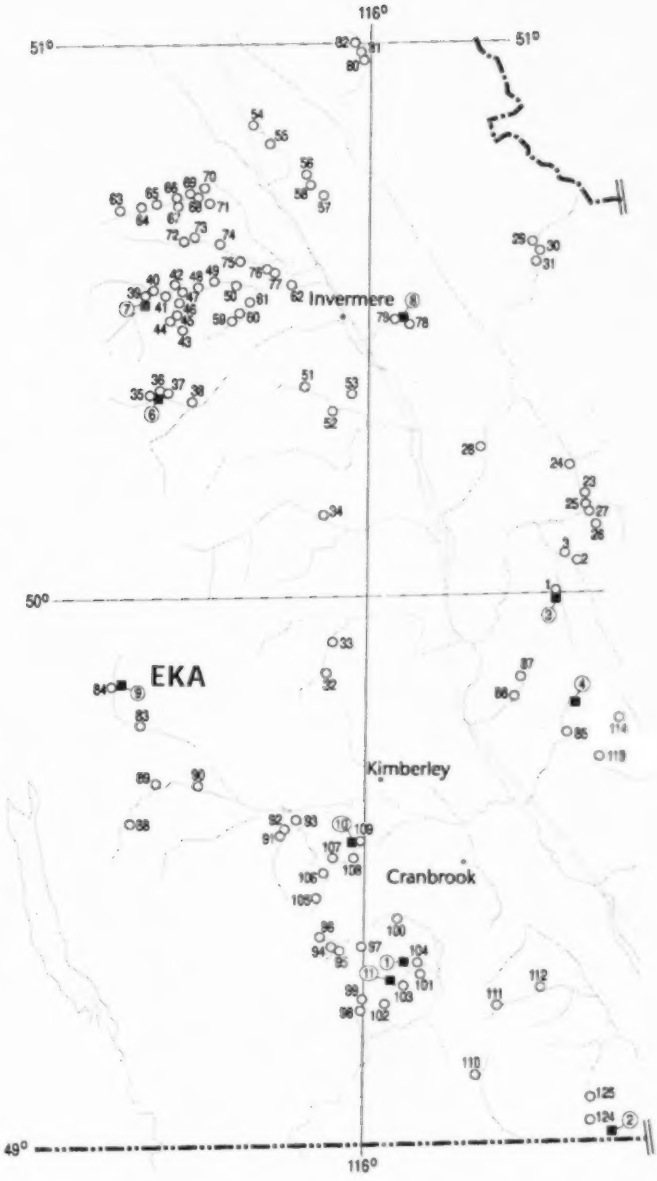
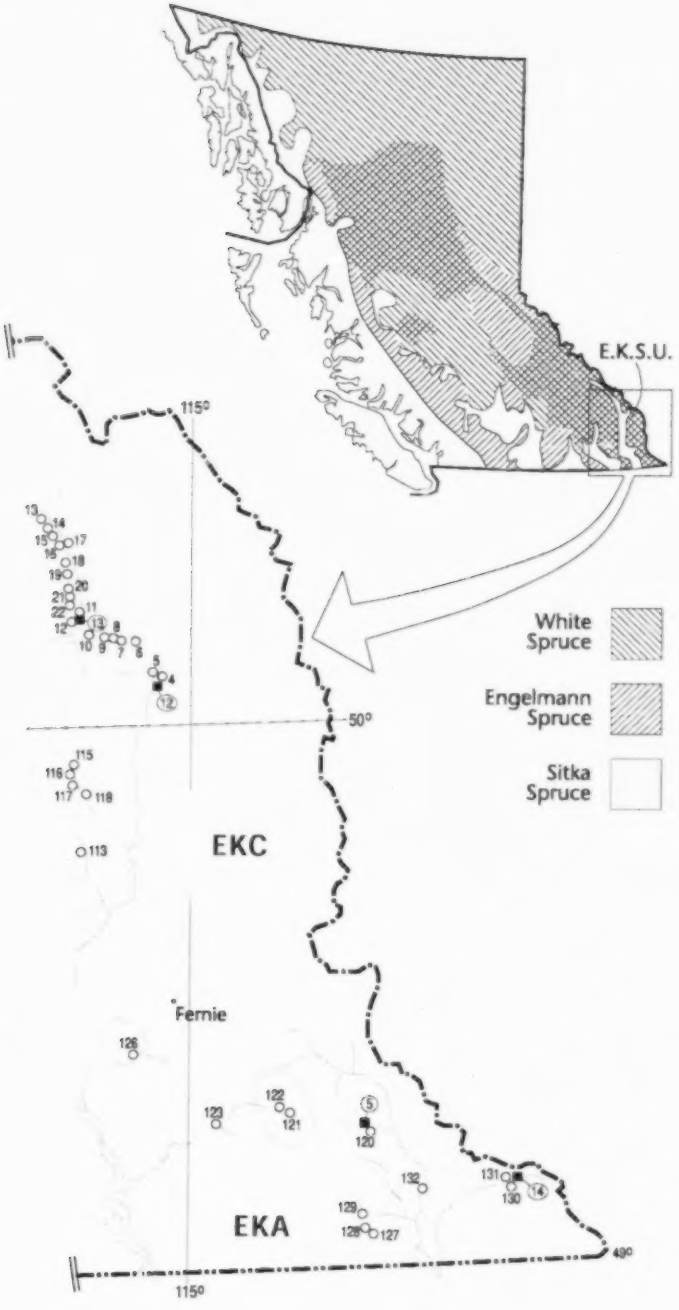


FIGURE 1
Geographic distribution of white-Engelmann spruce complex, locations of the East Kootenay Selection Unit, plus-trees (o) and progeny test sites (■), and division of East Kootenay Acidic (EKA) and Calcereous (EKC) zones.


E.K.S.U.
115°
50°
White Spruce
Engelmann Spruce
Sitka Spruce
EKC
EKA
Fernie
49°
115°

MATERIALS AND METHODS

SELECTION OF PLUS-TREES

The East Kootenay Selection Unit is located in the dry belt of the southeast corner of British Columbia, extending between latitudes 49° 00' to 50° 45' N and longitudes 114° 30' to 116° 30' W (Figure 1). Populations are mostly Engelmann spruce, with some influence of white spruce. A total of 132 plus-trees were selected along forest access roads in 1969 (Figure 1; Table 1), using visual size (height and diameter) as the primary selection criterion, and form and branching traits as the secondary criteria (Kiss 1976). The elevational distribution of these plus-trees varied from 853 to 2012 m. Open-pollinated seed was collected from 110 of these selections and the identity of seedlots was maintained by individual parent trees throughout the entire experiment.

ESTABLISHMENT OF PROGENY TRIALS

Fourteen open-pollinated progeny trials were established throughout the selection unit, and one was located at Red Rock, near Prince George, in 1975 using 2+1 bareroot seedlings (Figure 1; Table 2). Because of unfavourable environmental conditions following planting and heavy grass competition, initial survival at four test sites (Lamb Creek, Wildhorse, St. Mary, and Gold Hill Creek) was very poor. These trials were considered failures and were excluded from the present analysis. A randomized complete block design was employed at all test sites. A row plot of 10 seedlings with 2.5 m spacing represented a family within each block. Two to four blocks were planted and 104–110 families were tested at the 10 local sites, while seven blocks and 94 families were tested at Red Rock (Table 2).

DATA COLLECTION AND ANALYSIS

Height was measured to the nearest centimetre immediately following planting, and 3, 6, 10, 15, and 20 years thereafter. Diameter at breast height was measured to the nearest millimetre after 15 and 20 growing seasons in the field. Stem volume was estimated according to Kovats (1977). Survival was recorded as proportions of live trees per plot.

TABLE 1 *Geographic locations of selected plus-trees and average performance of their open-pollinated progeny 20 years after outplanting (numbers in brackets are probabilities of statistical significance of among-site differences, expressed as percentages)*

Family No.	Lat. (°N)	Long. (°W)	Elev. (m)	Height (cm)	Diameter (mm)	Volume (cm^3)	Survival (%)
*1	50.00	115.53	1615				
2	50.05	115.47	1372	395 (0.18)	56 (8.77)	6153 (20.6)	84 (0.01)
*3	50.07	115.52	1311				
4	50.13	115.10	1585	333 (1.06)	49 (0.88)	4711 (8.88)	75 (9.46)
5	50.15	115.12	1570	381 (0.01)	57 (0.01)	6612 (0.03)	78 (11.1)
6	50.17	115.15	1509	366 (0.02)	52 (0.01)	5270 (0.01)	84 (0.01)
7	50.17	115.18	1463	410 (1.17)	60 (0.13)	6921 (0.08)	82 (4.55)
*8	50.17	115.20	1417				
9	50.18	115.23	1372	409 (0.04)	64 (0.02)	8156 (0.07)	82 (4.46)
*10	50.17	115.25	1311				
*11	50.22	115.25	1311				
12	50.22	115.27	1250	394 (0.01)	55 (0.01)	6313 (0.01)	66 (0.73)
13	50.40	115.35	1524	326 (13.3)	49 (1.01)	3610 (1.07)	79 (5.65)
14	50.38	115.33	1524	292 (0.09)	40 (0.01)	2900 (0.06)	67 (8.57)
15	50.37	115.33	1524	315 (0.74)	44 (0.51)	3646 (1.62)	78 (14.4)
*16	50.35	115.33	1463				
17	50.35	115.32	1463	325 (4.01)	44 (3.49)	3744 (0.87)	74 (0.81)
18	50.33	115.30	1463	356 (0.49)	52 (0.14)	5099 (1.79)	69 (0.01)
19	50.30	115.30	1433	378 (0.17)	56 (0.01)	5583 (0.96)	81 (0.04)
20	50.25	115.27	1402	387 (0.45)	55 (0.29)	5583 (3.29)	80 (0.03)
21	50.23	115.28	1463	323 (14.2)	45 (8.14)	3280 (3.56)	77 (0.22)
*22	50.23	115.28	1463				
23	50.17	115.45	1158	387 (0.23)	53 (0.19)	6125 (0.19)	73 (3.35)
24	50.22	115.45	1128	386 (0.22)	55 (0.63)	5587 (0.05)	68 (0.71)
25	50.15	115.45	1158	367 (0.42)	55 (3.20)	5532 (2.12)	75 (2.46)
26	50.12	115.42	1402	337 (4.63)	48 (12.8)	4715 (31.0)	79 (0.01)
27	50.15	115.43	1219	396 (0.40)	55 (0.31)	5934 (6.00)	87 (3.10)
28	50.28	115.68	853	433 (1.30)	61 (3.17)	7841 (4.39)	86 (9.45)
29	50.62	115.55	1189	437 (0.09)	64 (0.04)	9378 (0.14)	81 (0.01)
30	50.62	115.55	1189	423 (0.01)	62 (0.01)	8204 (0.01)	84 (0.01)
31	50.60	115.55	1128	411 (0.39)	58 (0.35)	7409 (1.16)	82 (0.07)
32	49.87	116.08	1524	351 (0.90)	53 (0.24)	5293 (0.47)	82 (0.01)
33	49.93	116.08	1402	326 (1.90)	46 (0.33)	4035 (0.02)	78 (0.01)

TABLE 1 *Continued*

Family No.	Lat. (°N)	Long. (°W)	Elev. (m)	Height (cm)	Diameter (mm)	Volume (cm^3)	Survival (%)
34	50.15	116.10	1128	407 (0.01)	57 (0.02)	6958 (0.10)	84 (23.4)
35	50.37	116.48	1372	292 (1.16)	41 (0.28)	2631 (7.81)	67 (0.04)
36	50.37	116.45	1372	313 (0.07)	46 (0.01)	3700 (0.46)	76 (0.05)
*37	50.37	116.45	1372				
38	50.35	116.42	1341	351 (0.08)	53 (0.02)	5555 (0.11)	78 (2.73)
39	50.55	116.52	1311	379 (9.12)	54 (9.47)	5412 (19.3)	85 (4.44)
40	50.55	116.50	1280	420 (0.06)	62 (0.07)	8303 (0.78)	75 (3.93)
41	50.55	116.48	1250	360 (0.04)	54 (0.07)	5451 (0.87)	85 (0.34)
42	50.57	116.45	1250	360 (2.05)	52 (15.9)	5398 (30.3)	80 (18.6)
43	50.50	116.43	2012	293 (-[a])	58 (-)	3244 (-)	50 (-)
*44	50.52	116.45	1859				
45	50.52	116.45	1768	265 (49.9)	36 (44.9)	1965 (27.6)	50 (25.8)
46	50.53	116.43	1676	321 (22.2)	47 (37.9)	4085 (43.3)	70 (0.01)
47	50.55	116.43	1615	319 (0.12)	43 (0.03)	3585 (0.52)	60 (0.01)
48	50.57	116.38	1158	427 (0.01)	62 (0.01)	8218 (0.06)	88 (0.21)
49	50.57	116.33	1128	408 (0.17)	60 (0.05)	7330 (0.40)	79 (0.43)
50	50.57	116.30	1128	370 (0.01)	53 (0.01)	6185 (0.01)	79 (0.80)
51	50.38	116.10	1433	325 (0.01)	48 (0.01)	4014 (0.01)	63 (3.92)
52	50.35	116.07	1280	371 (2.90)	55 (4.40)	5762 (1.00)	61 (2.41)
53	50.37	116.03	1524	383 (0.05)	57 (0.01)	6240 (0.01)	85 (7.10)
54	50.87	116.23	1463	329 (-)	47 (-)	3589 (-)	93 (-)
55	50.83	116.18	1311	410 (1.83)	61 (3.86)	8279 (5.55)	83 (0.02)
*56	50.77	116.12	1311				
57	50.73	116.05	1433	371 (0.02)	56 (0.11)	6216 (0.32)	85 (1.19)
58	50.75	116.08	1341	370 (0.04)	56 (0.16)	6673 (3.79)	76 (1.08)
59	50.50	116.28	1737	283 (0.01)	40 (0.03)	2698 (0.30)	61 (0.01)
*60	50.52	116.27	1615				
61	50.53	116.27	1463	364 (52.3)	52 (64.7)	5392 (68.2)	59 (0.06)
62	50.53	116.13	1006	421 (6.03)	60 (13.1)	8542 (12.3)	88 (8.58)
63	50.68	116.60	1646	250 (7.27)	32 (7.12)	2203 (21.0)	37 (0.27)
64	50.70	116.53	1585	295 (0.06)	43 (0.02)	3274 (0.01)	56 (0.01)
65	50.72	116.47	1311	322 (1.85)	47 (0.87)	3645 (1.09)	62 (0.01)
66	50.72	116.45	1341	308 (0.65)	44 (1.76)	3369 (0.65)	63 (0.01)
67	50.72	116.45	1341	309 (0.28)	42 (0.34)	3039 (0.45)	68 (0.41)
68	50.73	116.42	1311	360 (0.19)	52 (1.07)	6406 (11.2)	80 (0.24)
69	50.73	116.40	1280	358 (0.01)	56 (0.01)	6096 (0.01)	86 (0.13)

TABLE 1 *Continued*

Family No.	Lat. (°N)	Long. (°W)	Elev. (m)	Height (cm)	Diameter (mm)	Volume (cm^3)	Survival (%)
70	50.75	116.38	1219	435 (0.53)	64 (3.37)	8482 (2.03)	82 (0.60)
71	50.73	116.35	1189	407 (0.01)	57 (0.01)	6871 (0.01)	82 (1.71)
72	50.63	116.43	1463	290 (2.00)	38 (1.07)	3250 (0.01)	50 (7.31)
*73	50.65	116.42	1433				
74	50.63	116.33	1402	307 (3.37)	42 (0.83)	3534 (4.86)	72 (0.09)
75	50.62	116.27	1311	434 (0.12)	63 (0.07)	9260 (0.03)	72 (0.01)
76	50.62	116.23	1128	415 (0.01)	59 (0.01)	7533 (0.01)	69 (9.45)
77	50.58	116.20	1067	377 (1.11)	54 (3.11)	6163 (9.65)	87 (3.20)
78	50.47	115.83	1280	418 (0.19)	59 (0.23)	7859 (15.0)	81 (0.09)
79	50.48	115.87	1189	409 (15.2)	56 (14.4)	6106 (17.2)	85 (40.8)
80	50.95	116.15	1250	389 (1.44)	57 (0.59)	6845 (0.56)	90 (10.2)
81	50.95	116.17	1250	401 (0.04)	58 (0.04)	7045 (0.02)	84 (2.57)
82	50.97	116.18	1250	354 (0.08)	52 (0.55)	4745 (0.48)	76 (0.01)
83	49.77	116.53	1250	313 (0.34)	41 (0.22)	3306 (1.41)	63 (0.76)
*84	49.80	116.60	1341				
85	49.75	115.52	1280	376 (0.01)	53 (0.01)	5702 (0.18)	88 (50.2)
86	49.80	115.60	1676	304 (27.8)	39 (24.7)	2777 (62.6)	57 (13.0)
87	49.82	115.60	1615	331 (0.15)	46 (0.03)	4262 (0.10)	65 (0.11)
88	49.62	116.57	1372	352 (0.06)	50 (0.24)	5192 (0.13)	78 (0.24)
89	49.67	116.45	1402	334 (0.35)	47 (0.34)	5132 (2.19)	68 (12.6)
90	49.65	116.40	1250	381 (0.16)	54 (0.09)	5614 (0.05)	76 (0.02)
91	49.57	116.18	1372	282 (0.03)	37 (0.05)	2716 (0.01)	73 (1.79)
92	49.58	116.18	1219	343 (0.28)	50 (0.53)	4115 (5.01)	68 (4.92)
93	49.58	116.13	1250	384 (0.79)	49 (1.34)	6043 (11.2)	78 (75.4)
94	49.37	116.10	1554	303 (0.52)	43 (0.18)	3644 (10.8)	61 (20.9)
95	49.35	116.10	1554	343 (0.02)	50 (0.04)	4595 (2.60)	75 (0.08)
96	49.37	116.12	1554	338 (3.70)	47 (6.96)	4830 (4.12)	75 (15.2)
97	49.35	116.05	1694	343 (0.69)	48 (0.96)	4658 (2.94)	67 (4.67)
*98	49.28	116.07	1737				
*99	49.28	116.07	1694				
100	49.42	115.97	1341	333 (3.81)	48 (3.32)	4649 (7.51)	69 (0.35)
101	49.33	115.88	1067	327 (0.01)	46 (0.01)	4382 (0.01)	73 (0.07)
102	48.30	115.98	1494	365 (5.24)	53 (1.96)	6061 (4.03)	72 (23.8)
103	49.30	115.92	1189	341 (0.07)	47 (0.11)	4405 (0.52)	84 (0.04)
104	49.33	115.88	1128	344 (0.05)	48 (0.01)	4786 (0.13)	85 (2.22)
105	49.43	116.13	1524	347 (0.08)	54 (0.01)	5932 (0.04)	80 (2.87)

TABLE I *Concluded.*

Family No.	Lat. (°N)	Long. (°W)	Elev. (m)	Height (cm)	Diameter (mm)	Volume (cm^3)	Survival (%)
106	49.47	116.10	1463	317 (0.01)	45 (0.01)	4194 (1.25)	78 (0.01)
107	49.48	116.10	1402	314 (1.47)	44 (1.43)	3863 (10.7)	61 (0.11)
108	49.50	116.07	1341	340 (0.01)	46 (0.01)	4558 (0.01)	80 (0.18)
109	49.53	116.05	1280	364 (0.01)	49 (0.01)	5917 (0.76)	74 (0.02)
110	49.17	115.77	1615	305 (3.87)	42 (5.97)	3434 (3.37)	85 (22.1)
111	49.23	115.70	1402	334 (0.02)	49 (0.01)	4689 (0.03)	78 (0.01)
112	49.27	115.65	1280	383 (0.18)	53 (0.13)	6306 (2.43)	73 (0.37)
113	49.78	115.35	1524	329 (0.29)	46 (0.10)	4068 (0.15)	66 (3.63)
114	49.77	115.43	1707	285 (0.10)	41 (0.01)	2963 (0.62)	75 (0.04)
115	49.92	115.28	1676	272 (1.71)	35 (1.40)	2555 (0.09)	66 (0.89)
116	49.92	115.28	1585	283 (0.19)	38 (0.05)	3007 (1.10)	53 (27.2)
*117	49.90	115.30	1524				
118	49.88	115.28	1463	322 (0.30)	45 (0.53)	3423 (11.5)	67 (0.10)
119	49.68	115.45	1585	292 (1.25)	40 (1.13)	2676 (7.13)	43 (0.13)
*120	49.27	114.63	1585				
121	49.30	114.75	1585	294 (0.60)	41 (0.08)	3059 (0.12)	59 (1.80)
*122	49.28	114.77	1494				
123	49.33	114.93	1219	379 (0.01)	49 (0.09)	4803 (0.07)	73 (3.36)
124	49.02	115.47	1524	343 (0.71)	49 (0.29)	4934 (2.59)	70 (7.73)
125	49.08	115.47	1250	327 (14.1)	43 (23.1)	3626 (12.4)	59 (9.27)
126	49.42	115.17	1097	336 (22.3)	47 (35.7)	3798 (31.8)	79 (0.01)
*127	49.07	114.60	1646				
*128	49.08	114.62	1707				
*129	49.10	114.62	1524				
*130	49.15	114.30	1494				
131	49.15	114.30	1524	311 (0.02)	43 (0.10)	3491 (0.89)	55 (1.23)
132	49.13	114.50	1311	391 (0.02)	59 (0.24)	6923 (4.06)	79 (7.19)

* Trees not tested at any of the sites due to lack of seedlings.
a Not enough degrees of freedom to perform test.

TABLE 2 *Geographic locations of test sites and average performance of open-pollinated progeny 20 years after outplanting (numbers in brackets are probabilities of statistical significance of among-family differences)*

Test site		Location					Performance			
I.D.	Name	Lat. (°N)	Long. (°W)	Elev. (m)	No. of reps.	No. of families	Height (cm)	Diameter (mm)	Volume (cm^3)	Survival (%)
*1	Lamb Creek	49.33	115.87	1160	2					
2	Bloom Creek	49.02	115.45	1676	2	110	425(0.01%)	66(0.01%)	7497(0.01%)	87(0.01%)
3	Lussier Creek	50.00	115.52	1554	2	110	304(0.01%)	37(0.01%)	2415(0.32%)	73(0.01%)
*4	Wildhorse Creek	49.82	115.48	1675	4					
5	Lodgepole	49.27	114.70	1646	2	110	279(0.06%)	39(1.17%)	2284(0.09%)	84(0.09%)
6	Jumbo Creek	50.37	116.48	1371	4	109	358(0.01%)	48(0.01%)	4210(0.01%)	75(0.01%)
7	Horsethief Creek	50.52	116.57	1402	2	108	349(0.01%)	48(0.17%)	4292(0.02%)	59(0.14%)
8	Windermere Creek	50.48	115.85	1585	2	108	297(0.54%)	37(3.07%)	2049(2.13%)	64(0.01%)
*9	St. Mary	49.80	116.60	1615	2					
10	Perry Creek	49.55	116.03	1463	3	108	484(0.30%)	75(3.68%)	12791(4.68%)	81(0.01%)
*11	Gold Hill Creek	49.33	115.90	1220	2					
12	East White River	50.15	115.10	1524	2	108	295(0.01%)	39(0.01%)	2321(0.01%)	86(0.01%)
13	Grave Creek	50.20	115.30	1402	2	107	304(0.01%)	41(0.01%)	3839(0.35%)	42(18.1%)
14	Roche Creek	49.18	114.30	1646	2	104	353(48.2%)	56(39.1%)	5897(20.2%)	70(0.01%)
15	Red Rock	53.75	122.73	762	7	94	451(0.01%)	71(0.01%)	10126(0.01%)	92(0.01%)

* failure plantations

The following analysis of variance (ANOVA) was performed treating plot as the experimental unit to examine the differences in cumulative height, diameter, stem volume, and survival among families at each site:

$Y_{ij} = \mu + F_i + B_j + \varepsilon_{ij}$,

where

Y_{ij} = observation of the i-th family in the j-th block,

μ = site mean,

F_i = effect of the i-th family,

B_j = effect of the j-th block,

ε_{ij} = experimental error (the effect of interaction between the i-th family and the j-th block).

This model was extended to test the differences among sites and families, and to assess the relative magnitude of site by family interaction:

$Y_{ijk} = \mu + F_i + S_j + B_k(S_j) + F_iS_j + \varepsilon_{ijk}$,

where

Y_{ijk} = observation of the i-th family in the k-th block at the j-th site,

μ = overall experiment mean,

F_i = effect of the i-th family,

S_j = effect of the j-th site,

$B_k(S_j)$ = effect of the k-th block at the j-th site,

F_iS_j = effect of interaction between the i-th family and the j-th site,

ε_{ijk} = experimental error (effect of interaction between the i-th family and the k-th block at the j-th site).

All effects in the ANOVA models were considered as random, and ANOVA was performed using the GLM procedure and the type III estimable functions (SAS Institute 1988). Simple linear regression analysis was employed to examine the elevational patterns of among-family variation. The logarithmic and arcsine transformations were applied to stem volume and survival, respectively, before ANOVA and regression analysis for the purpose of normality and variance homogeneity.

RESULTS AND DISCUSSION

After 20 growing seasons in the field, interior spruce from the East Kootenay Selection Unit reached an average height of 354 cm, a diameter of 51 mm, and a stem volume of 5247 cm^3. It

demonstrated an exponentially shaped average height growth curve during this period of juvenile development (Figure 2). Differences in the slope of the curves were noticeable among test sites, but were not statistically significant (p=0.8794, analysis of covariance [Bergerud and Sit 1991]). The height growth data fit the exponential models very well, with R^2 values greater than 96% for individual sites and sites averaged. The mean height growth curve (Figure 2) indicates that spruce grew very slowly during the first six growing seasons in the field, with an average increment of less than 7 cm per year. There was a significant increase in growth rate thereafter, and a 17 cm annual increment was maintained almost constantly until another significant increase in growth rate occurred (about 30 cm per year) 15 years after outplanting. This growth pattern is in general agreement with previous findings in Engelmann spruce. According to published data, spruce at these test sites grew faster than those in Colorado (about 120–150 cm tall 20 years after planting), but similar to those in Montana (which may be 140 cm tall 10 years after planting) (see Alexander and Shepperd 1991 for references). It was reported that Engelmann spruce will grow 100 mm in diameter in 10 years on the best sites in southern British Columbia (Smith 1950). The present study indicates that our test sites were below this standard.

The average survival after 20 years of outplanting was 73%. More than 85% of the mortality occurred during the first three seasons in the field (Figure 3). Some trees at Grave Creek were accidentally removed during an operational thinning in surrounding stands in 1988 (Dave Wallden, pers. comm.), which would mainly account for the high mortality observed in the 15-year assessment at this site (Figure 3). Except for Grave Creek, the age trends of survival were similar at all other test sites; that is, high mortality in the first three years and stabilized survival thereafter (Figure 3). Similar findings have also been reported for both natural stands (Alexander 1984) and plantations (Shepperd et al. 1981) of Engelmann spruce. Based on 10-year test results, Shepperd et al. (1981) concluded that the eventual success of an Engelmann spruce plantation could be predicted as early as two years after planting. Our test results agree quite well with their conclusion.

Overall family mean height, diameter, stem volume, and survival ranged from 250 to 437 cm, 32 to 64 mm, 1965 to

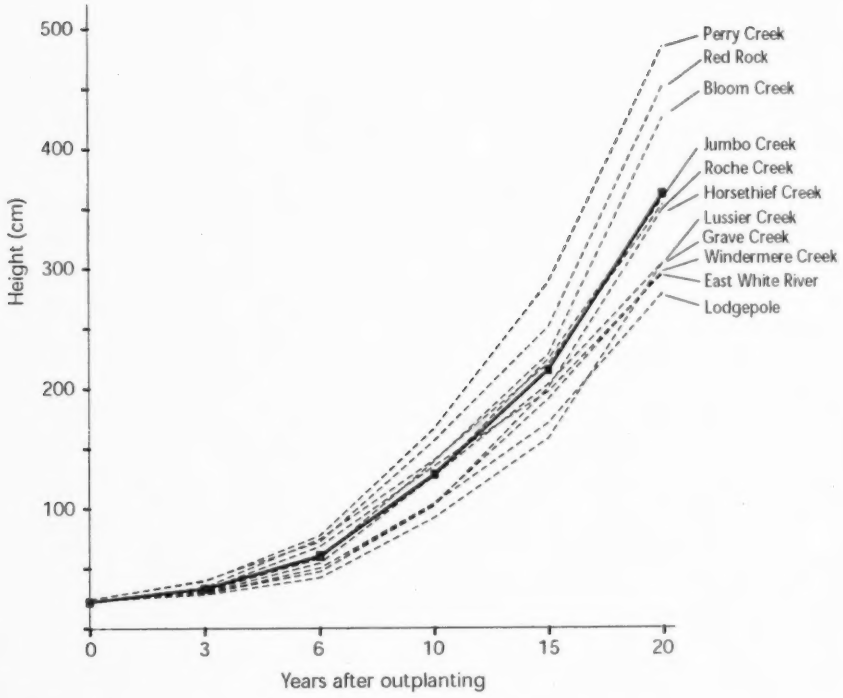


FIGURE 2 *Age trends of average height, overall (solid line) and at individual sites (broken lines).*

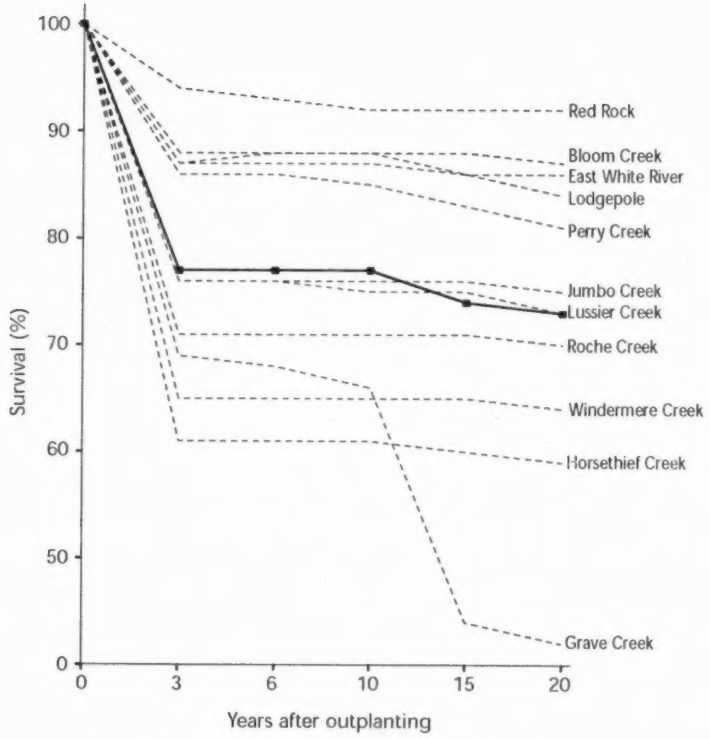


FIGURE 3 *Age trends of average survival, overall (solid line) and at individual sites (broken lines).*

9378 cm^3, and 37 to 93%, respectively, 20 years after outplanting (Table 1). Variation among families was statistically significant for all the traits at all the sites except for growth at Roche Creek and survival at Grave Creek (Table 2). Among-family differences accounted for 9–19% of the total variation observed in the entire experiment (Table 3). Growth and survival were positively associated (Figure 4), indicating that fast-growing families were also good survivors. While performance differed significantly ($p<0.05$) across test sites for most families (Table 1), superior families tended to be less affected by test environments, as suggested by the negative correlations between growth and survival and their corresponding coefficients of variation among test sites (Figure 5). These results demonstrate that superior families not only grew faster and survived better, but also performed more uniformly across different site environments.

Previous short-term provenance tests indicate that environmental pressures associated with elevation have been principal factors resulting in adaptive differentiation of interior spruce populations, and that variation in growth and other adaptive characters displayed gentle clines along elevation (Roche 1969; Dietrichson 1971; Nienstaedt et al. 1971; Rehfeldt 1994). In this study, significant negative elevational clines were detected for all the traits at all the test sites. The clines were parallel among test sites ($p = 0.9925$, analysis of covariance [Bergerud and Sit 1991]). Those elevational patterns became very strong when families were grouped into elevational bands. For instance, when families were assigned into seven elevational bands[1], 87% (survival) to 97% (height) of the among-band variation could be explained by elevation alone (Figure 6). Results from common garden study indicated that populations in the Intermountain West must be separated by at least 700 m before genetic differentiation in height growth becomes significant ($p<=0.20$) (Rehfeldt 1994). Using the same criterion (i.e., least significant difference among populations at 20% significance level), significant difference could be detected between the East Kootenay populations that are 125, 155, 152, and 227 m apart in elevation for height, diameter, stem volume, and survival, respectively (Figure 6). According to these results, interior spruce seed sources in the East Kootenays must not be transferred more than 230 m up or more than 150 m down, which is more restrictive than the current seed transfer limits (400 m upwards and 200 m downwards [British Columbia Ministry of Forests 1995]).

1 band 1: elevation below 1150 m, n=12; band 2: elevation 1150–1250 m, n=22; band 3: elevation 1250–1350 m, n=19; band 4: elevation 1350–1450 m, n=16; band 5: elevation 1450–1550 m, n=20; band 6: elevation 1550–1650 m, n=13; band 7: elevation above 1650 m, n=8.

TABLE 3 *Variance components (VC) and probability of statistical significance (p>F) from combined ANOVA*

Source of variation	d.f.	Height (cm)		Diameter (mm)		Volume (logarithm)		Survival (arcsine)	
		VC(%)	*p>F*	VC(%)	*p>F*	VC(%)	*p>F*	VC(%)	*p>F*
Site	10	45	0.0001	48	0.0001	44	0.0001	35	0.0001
Block within Site	19	4	0.0001	3	0.0001	4	0.0001	2	0.0001
Family	109	14	0.0001	9	0.0001	12	0.0001	19	0.0001
Site x Family	1059	5	0.0001	5	0.0001	5	0.0001	6	0.0001
Error	1831	32		35		35		38	

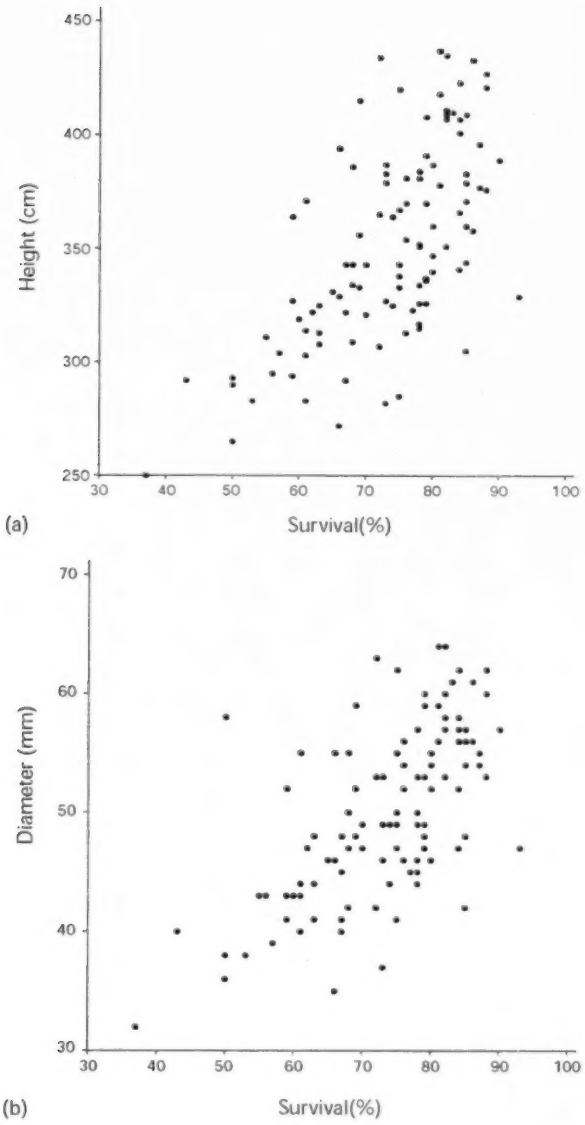
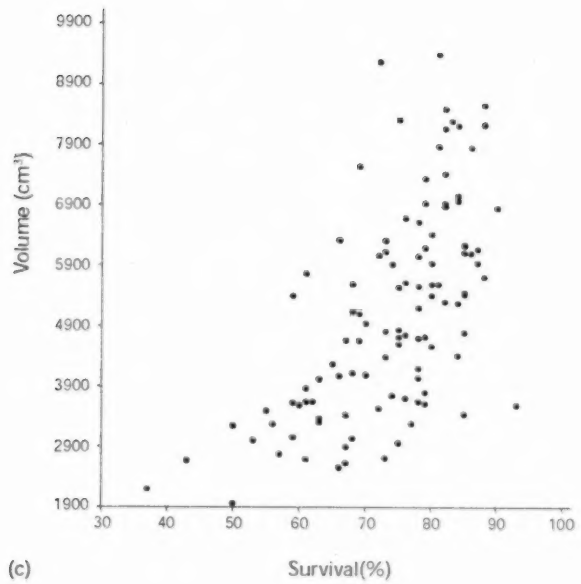
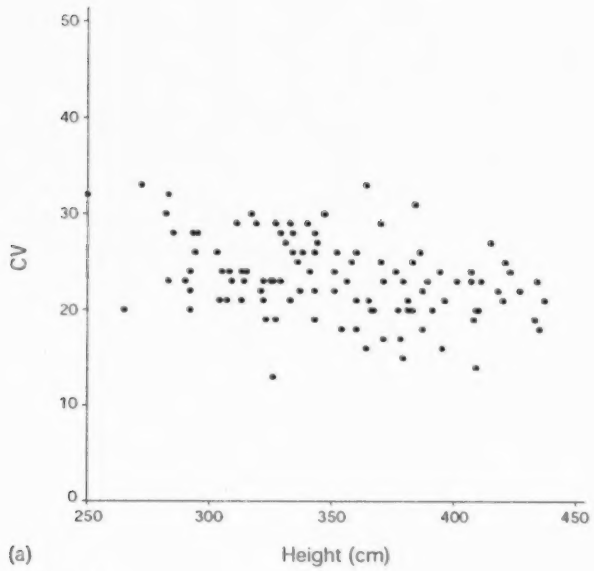


FIGURE 4 *Relationships between family mean growth and survival 20 years after outplanting.*



(c)

FIGURE 4 *Continued*



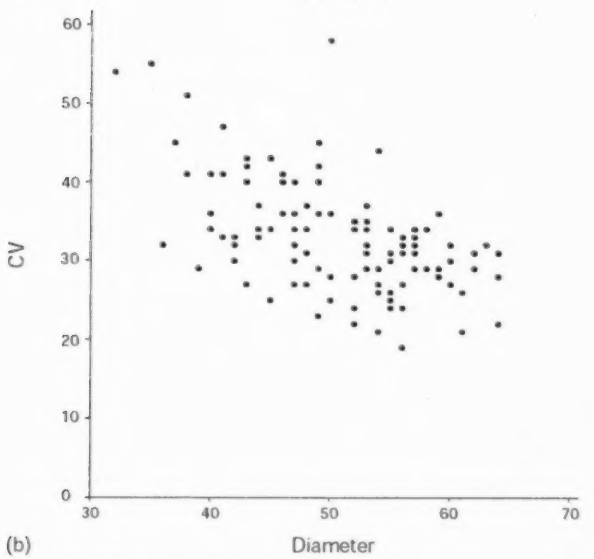
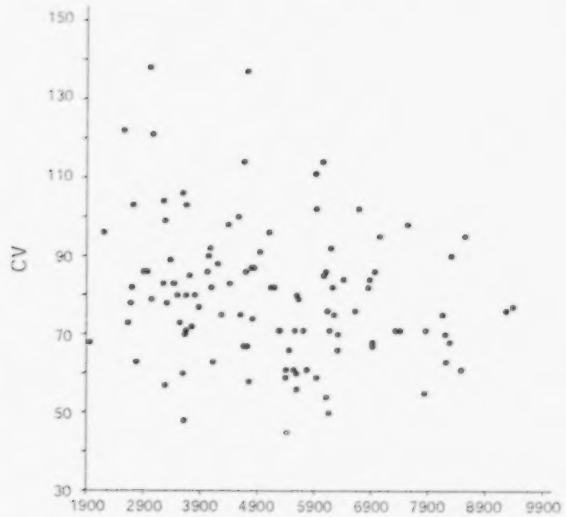


FIGURE 5 *Relationships between the coefficient of variation among test sites (CV) and cumulative family mean growth and survival.*



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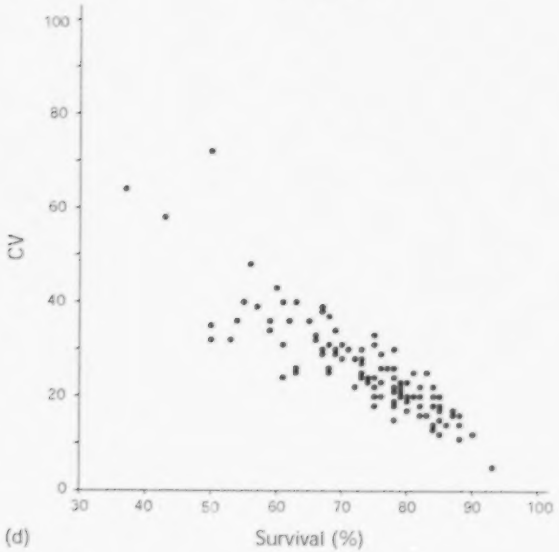
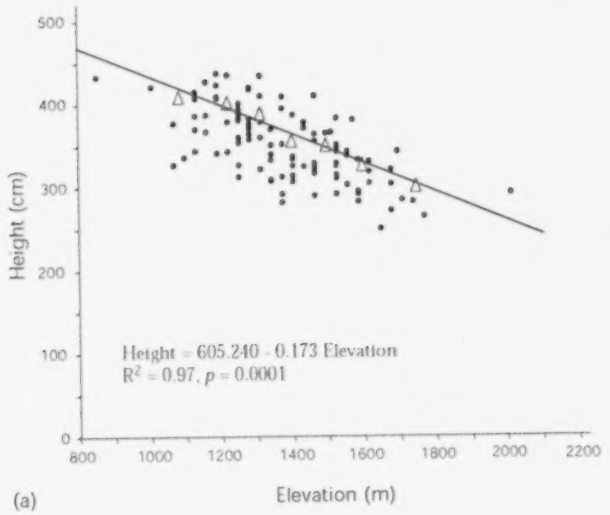
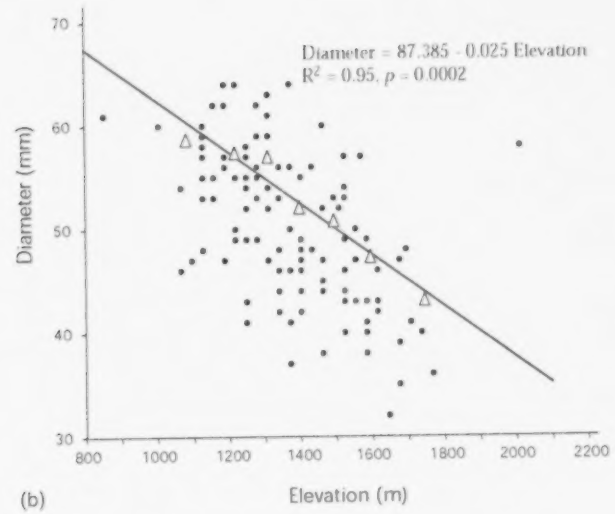


(d)

FIGURE 5 *Continued*

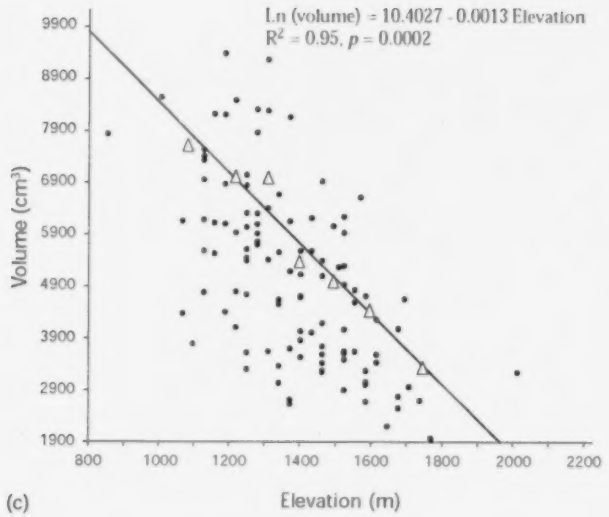


(a)



(b)

FIGURE 6 *Elevational clines in growth and survival (•: family means; Δ: elevational band means). Regression models are based on elevational band means.*



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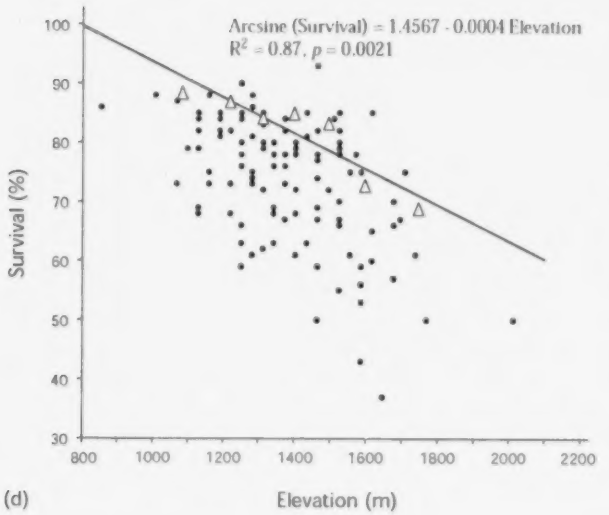

(d)

FIGURE 6 *Continued*

Variation in growth and survival among test sites was even greater. Site means ranged from 279 to 484 cm, 37 to 75 mm, 2049 to 12791 cm^3, and 42 to 92% for height, diameter, stem volume, and survival, respectively (Table 2). Differences among test sites were statistically highly significant and accounted for 35–48% of the total variation (Table 3).

There have been numerous studies demonstrating that site environment (e.g., weather, topography, site preparation, chemical and physical soil conditions, vegetation, and other biotic factors) has great impact on the growth and survival of interior spruce (see Alexander and Shepperd 1991 for references). Field observation indicates that drought and weed competition were two major factors determining the establishment and growth of interior spruce in the east Kootenays. Spruce at drier (e.g., Windermere Creek) and bushier (e.g., Horsethief Creek) sites suffered higher mortality and grew slower. Even within a site, trees in drier patches (e.g., Perry Creek) and blocks (e.g., Block 27 at Jumbo Creek and Block 17 at Grave Creek) displayed inferior performance. The high mortality in the four failure plantations was largely due to strong weed competition.

Soil chemical conditions appeared to have great influence on the growth and survival of interior spruce. According to previous seed planning zone designation, the East Kootenay Selection Unit is divided into East Kootenay Acidic (EKA) and East Kootenay Calcareous (EKC) seed planning zones based on the acidity of soil (Figure 1). Results indicate that trees from the EKC zone were superior in both growth and survival to those from EKA zone in whichever zone they were planted (Figure 7). However, trees at EKA sites grew faster (32% on average) and survived better (8% on average) than those at EKC sites, regardless of their origin (Figure 7). Although these differences were still small, they had been increasing as the test proceeded (Figure 8). Twenty years after outplanting, growth differences (height, diameter, and stem volume) between EKA and EKC sites had become statistically significant. Superior growth on acidic soil has also been reported in white spruce in eastern Canada (Teich and Holst 1974). At age 15 (from seed), trees from the same provenances planted at an acidic site (granitic parent material soil, pH=4.7) were 16% taller than at a calcareous site (limestone parent material soil, pH=6.6), which is remarkably similar to the observation in the present study. It has also been reported that

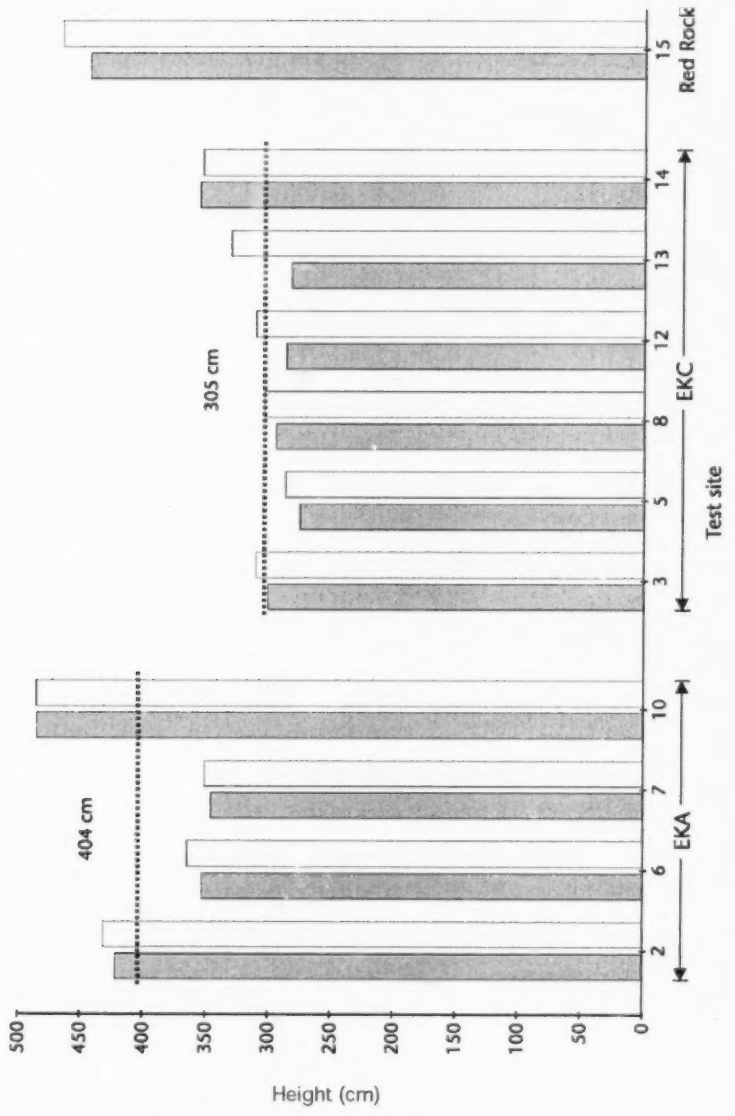

FIGURE 7 *Average height and survival of families from EKA (dark bars) and EKC (light bars) zones at EKA and EKC test sites 20 years after outplanting.*

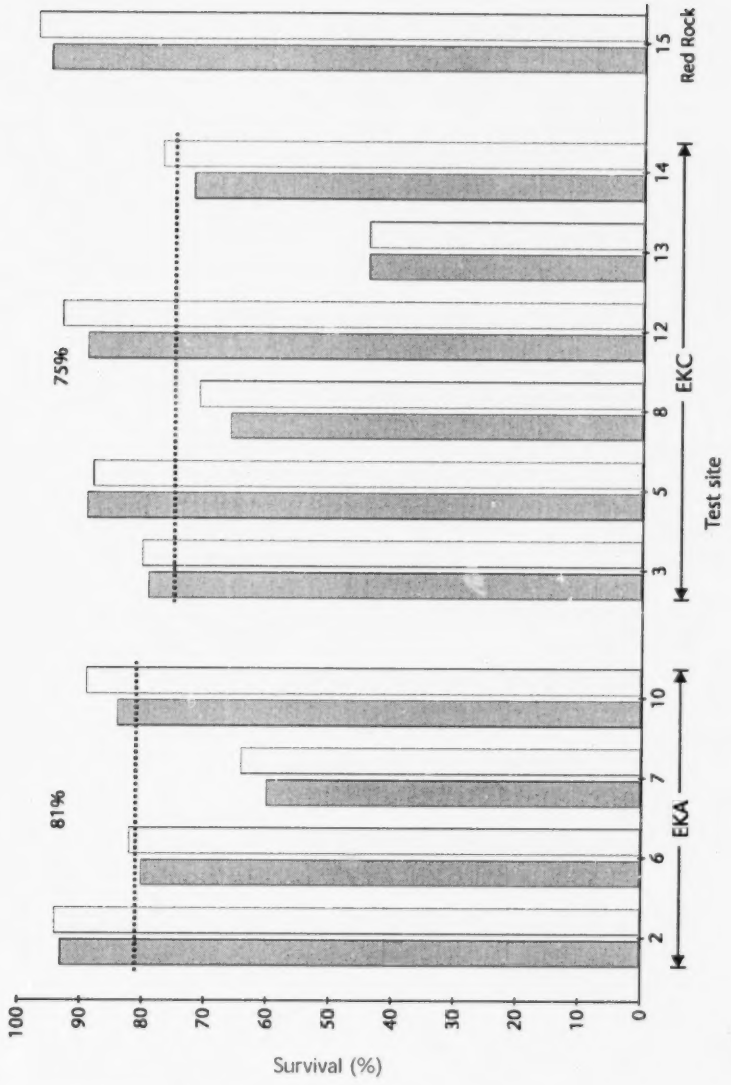

FIGURE 7 *Continued*

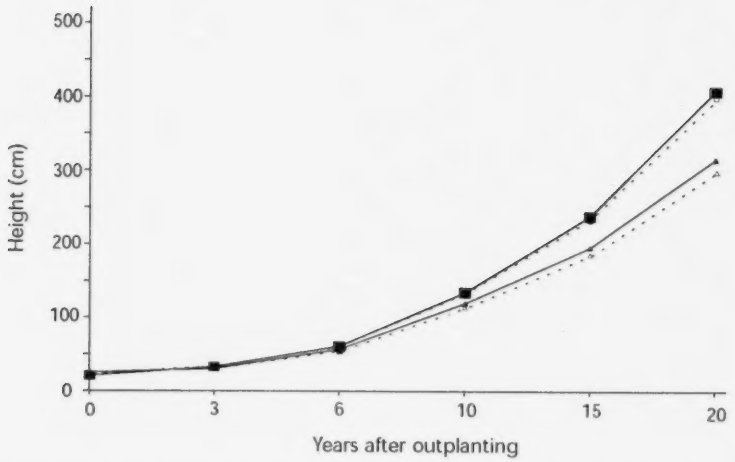

FIGURE 8 *Age trends of average height of families originated from EKA (broken lines) and EKC (solid lines) zones and planted at EKA (■) and EKC (Δ) sites.*

white spruce populations in eastern Canada have differentiated into limestone and non-limestone ecotypes (Teich and Holst 1974). The present study indicates that such differentiation has not occurred among populations of interior spruce in the East Kootenays (i.e., Engelmann spruce populations). Although it is not clear why trees from calcareous soil tended to be superior, it was not due to differences in the elevation of their origin. The average elevation of EKA and EKC family origins was not significantly different (p=0.5015) and, in fact, the former is marginally lower (1367 m and 1392 m, respectively). Whatever the underlying mechanisms that have generated these differences, the silvicultural significance is obvious: planting spruce at acidic sites (EKA) promises superior growth and survival, and seeds from the EKC zone are preferred no matter where they will be planted.

It is notable that interior spruce from the East Kootenays displayed the best survival and the second-highest growth rate at Red Rock, even though families were transferred about 4 degrees northwards and more than 7 degrees westwards from their average origin. Such outstanding performance may be partially attributed to more intensive silviculture treatment (e.g., better site preparation and maintenance) at this site. However,

the test results at least suggest that interior spruce in southeastern B.C. has the biological potential to be successfully used for reforestation in the central region of the province far exceeding the current seed transfer limits (2 degrees northwards and 5 degrees westwards [British Columbia Ministry of Forests 1995]).

Family–site interaction was statistically highly significant and accounted for 5% of total variation on average (Table 3). Because studying genotype–environment interaction through conventional analysis of variance has important disadvantages, and statistically significant interaction may be generated even if there is no true interaction (i.e., rank change of genotypes among environments [Burdon 1977]), the detected significant family–site interaction variances (Table 3) only suggest, but not warrant, the existence of true significant family–site interaction. Variation in the relative performance of interior spruce families among test sites in the East Kootenays will be examined using more sophisticated methods and will be reported elsewhere.

CONCLUSIONS

Interior spruce in the East Kootenays demonstrated great variation in growth and survival both among families and among test sites, indicating that using genetically superior material and choosing suitable sites are both important to reforestation success. Better growth and survival are expected by planting spruce from the East Kootenay Calcareous Zone at the acidic sites. Genetic differentiation along elevation was strongly clinal, yet the performance at Red Rock was excellent. Seed transfer along elevation should be restricted to 230 m upwards and 150 m downwards but transferring seed sources across geographic regions can be as far as 4 degrees northwards and 7 degrees westwards. Most of the mortality occurred in the first few years after outplanting; thus, care taken in site preparation, and stock raising, handling, and planting, as well as protecting new plantings against damaging agents, is crucial to the success of interior spruce plantations.

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